ACANTHODIAN FISH REMAINS FROM THE UPPER SILURIAN OR LOWER DEVONIAN OF THE AMAZON BASIN, BRAZIL

by P. JANVIER *and* J. H. G. MELO

ABSTRACT. Acanthodian spines, scales, and tooth whorls are described from the Pitinga Member of the Trombetas Formation (Middle Amazon Basin, northern Brazil). The spines and dermal scutes are of climatiid type, but the associated tooth whorl is more like that of an ischnacanthid. This acanthodian assemblage is quite similar to that from the top of the Catavi Formation of Bolivia, where an association of thelodont scales suggests an Early Devonian age. The new acanthodian remains from Brazil are unlikely to be older than the latest Silurian, thus refuting previous ideas that the richly fossiliferous Pitinga Member was Ordovician in age.

THE fossils described here were collected in the north-western portion of the State of Pará (northern Brazil), in a region where the Trombetas River and its major tributary, the Mapuera River, cross the belt of outcrops of Siluro-Devonian rocks that delineates the northern flank of the Middle Amazon Basin (text-fig. 1). Most of the fish remains were recovered from a core sample of the well SM-504, a shallow borehole drilled by Enge-Rio Engenharia e Consultoria S.A., near Cachoeira da Porteira village, in the outcrop of the upper section of the Pitinga Member of the Trombetas Formation. A bone-bed was encountered at a depth of 28·60 m within a thick layer of grey, fine-grained sandstone. The upper and lower surfaces of the fossiliferous sample have been prepared by removing the bone fragments and cleaning their natural moulds with dilute hydrochloric acid, after which a silicone cast was made from both surfaces (text-fig. 2), showing acanthodian scales, spines, scutes, and a tooth whorl. In addition, an isolated acanthodian spine (text-fig. 3B, C) was found along with bony fragments in siltstones which crop out at a cascade of the Sucuriju Creek (text-fig. 1), some 26 km to the west-south-west of well SM-504. It may belong to the same form as the spines in the core sample, thus suggesting that the same bone-bed may be followed over a relatively large distance.

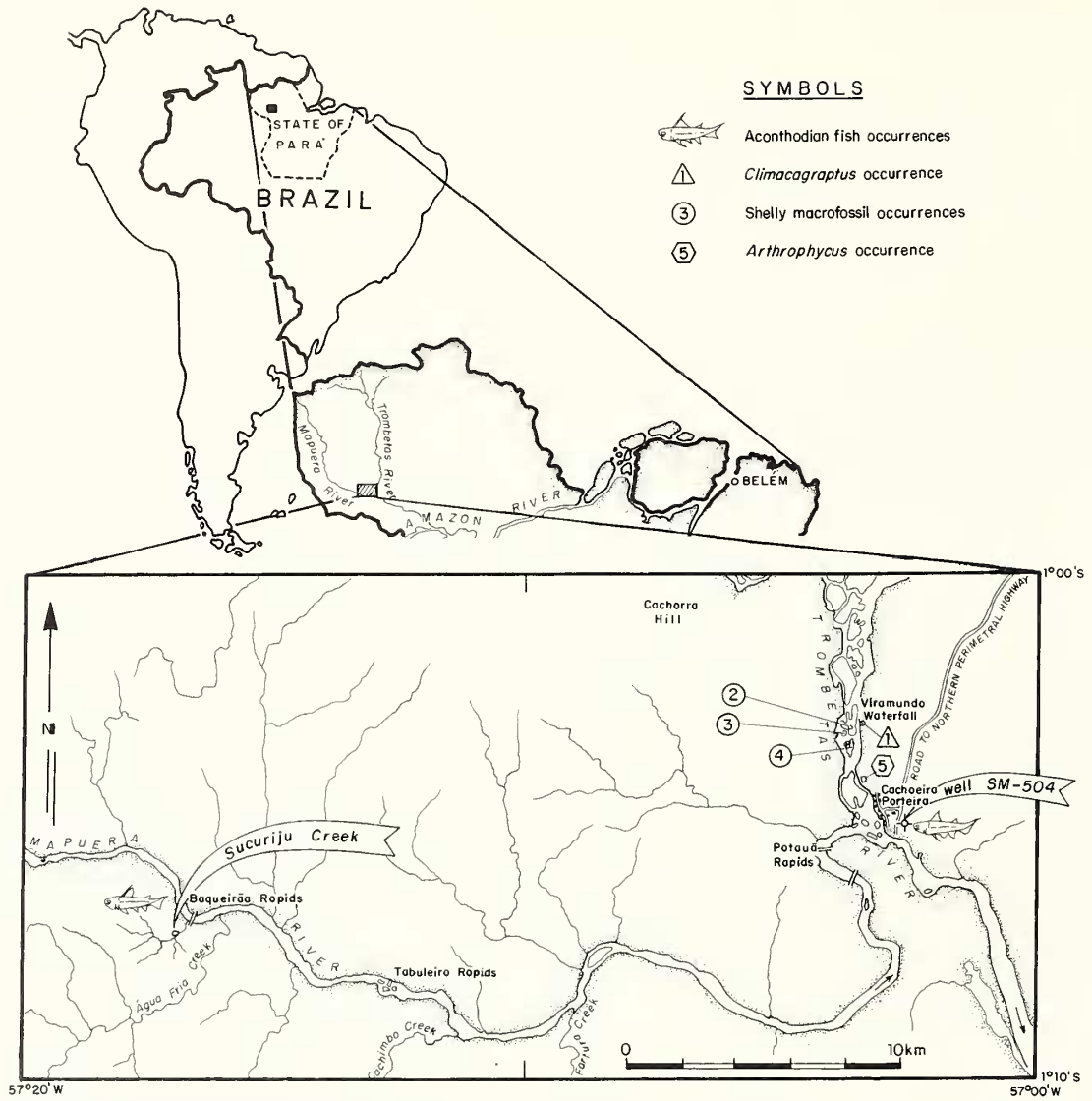
These fossils are interesting because of the scarcity of Middle Palaeozoic vertebrate remains in Brazil. For a long time, the only record of Devonian vertebrates from this country included mentions, but not illustrations, of possible *Machaeracanthus* spines and *Pteraspis* plates from the Maecuru Formation of the Middle Amazon Basin (Katzer 1897*a*, *b*), and spines from the Parnaíba Basin (Pimenteira Formation) assigned to such genera as *Ctenacanthus*, *Machaeracanthus*, and '*Devoncanthus*' (*sic*) (Kegel 1953, 1957; Santos 1961; Guimaraes 1964; Mendes 1971; Copper 1977). Leonardi (1982, 1983) described a tetrapod footprint from the Upper Devonian of the Parana Basin, and Janvier and Melo (1987) recorded some isolated actinopterygian scales from the Late Devonian shales of the Upper Amazon Basin.

All fossil material under considereration is housed in the collection of Petrobrás (Museu de Paleontologia do Cenpes, Rio de Janeiro, Brazil), under register numbers CENPES 002-V and 003-V.

DESCRIPTION

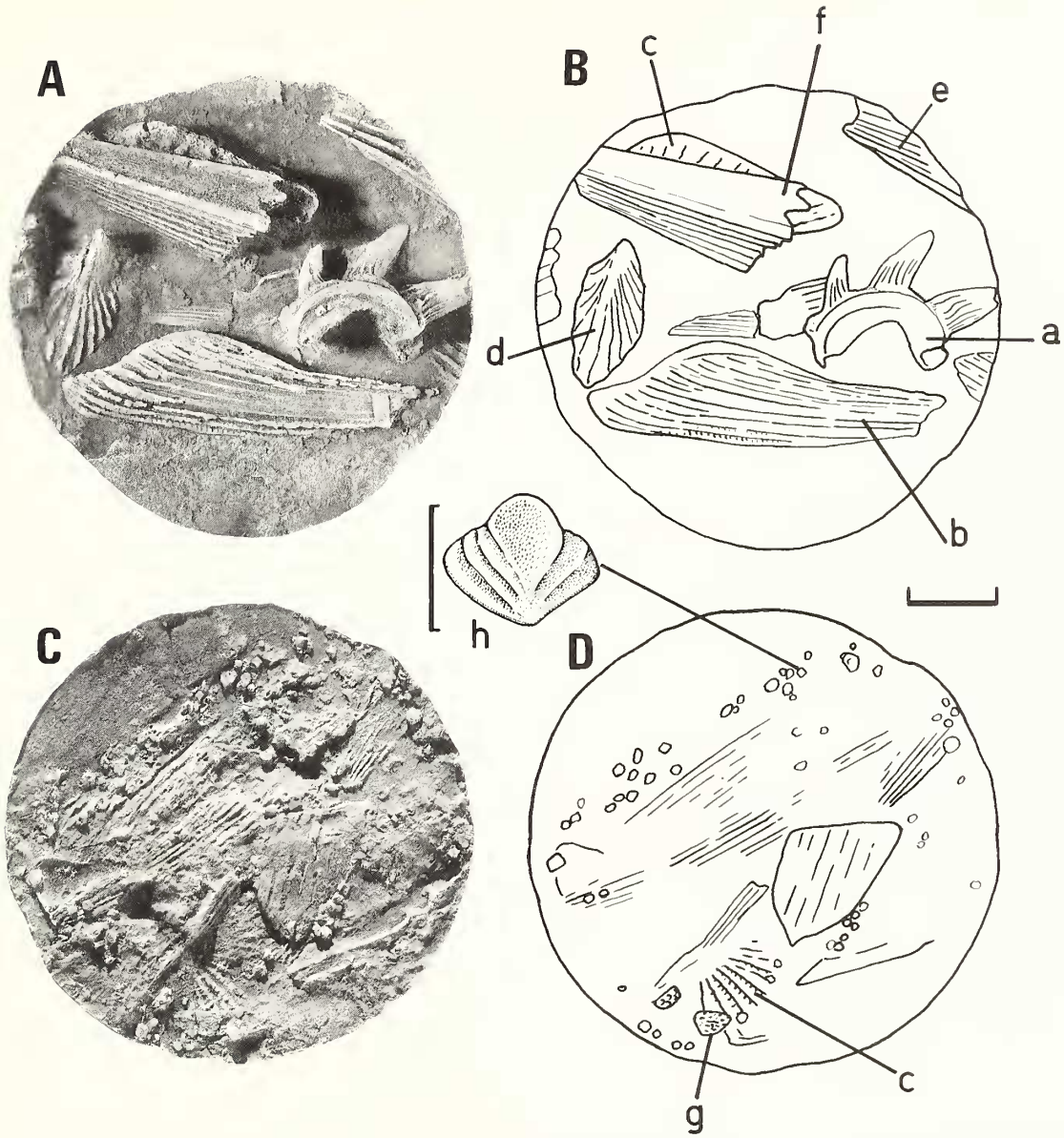
On one surface of the core sample from well SM-504, the cast shows several more or less complete spines and a large tooth whorl (text-fig. 2A, B). The most complete spines are a pectoral spine (b in text-fig. 2B) and an intermediate spine or scute (d). A fragmentary spine with a broad posterior surface (f) is probably a median

[Palaeontology, Vol. 31, Part 3, 1988, pp. 771–777.]



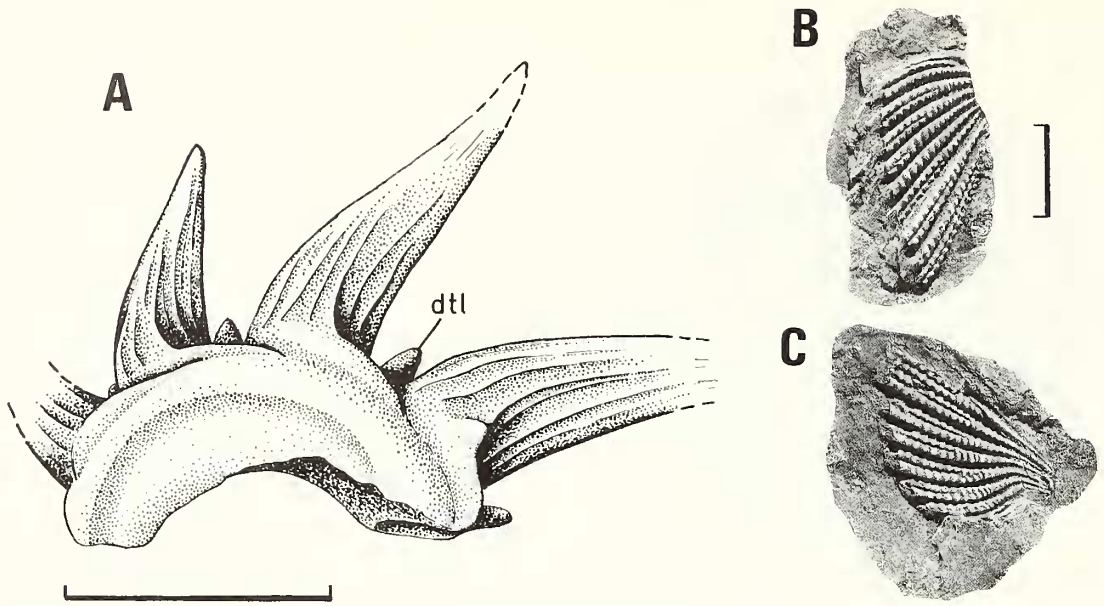
TEXT-FIG. 1. Locality map. Numbers refer to fossil sites mentioned in text: 1, Pitinga Member, basement contact outcrop at the Viramundo Waterfall; 2, Madame Island; 3, Praia Lisa Island; 4, Bota Island; 5, Caramujo locality. Fossils occurring in each locality are indicated by symbols shown in the figure.

fin spine, as is another fragment ornamented with very straight ridges (e). Finally, a broad-based spine (c), ornamented with strongly divergent ridges which are visible on the counterpart (c in text-fig. 2D), is most probably a prepectoral spine. The tooth whorl (a) bear three teeth and the base of a fourth one. The teeth are strongly bent posteriorly, and ornamented with sharp ridges, which become sinuous near the base laterally. There are very small lateral denticles on one side only (dtl in text-fig. 3A); on the opposite side of the main teeth, these denticles are replaced by shallow sharp ridges which prolong the flange of each tooth posteriorly. Such an asymmetry is also visible on the bony support of the whorl, which is embayed posteriorly by a deep notch. Such morphology may indicate that this tooth whorl did not occupy a median, symphysial position, but rather a parasymphysial position.



TEXT-FIG. 2. Acanthodian remains from well SM-504, Pitinga Member of the Trombetas Formation, State of Pará, Brazil (specimen no. Cenpes 002-V). A, B, lower surface of the core sample; silicone cast (A) and explanatory scheme (B). C, D, upper surface of the core sample; silicone cast (C) and explanatory scheme (D). Scale: 10 mm for A and B, and 1 mm for h. Identifiable remains: a, tooth whorl; b, pectoral fin spine; c, prepectoral spine; d, intermediate spine; e, f, median fin spines; g, possible plate of sclerotic ring or dermal bone of the cheek; h, scale in external view.

Ornamentation of the spines consists of relatively thin, sharp ridges, except on the intermediate and prepectoral spines, where the ridges are smoother and more irregular in shape. The pectoral spine displays about thirteen ridges on one side at the base. In places, particularly near the insertion base of the spines, these ridges are noded, the nodes often being set closely together.



TEXT-FIG. 3. A, reconstruction of the tooth whorl in text-fig. 2A, B, showing the lateral denticles (dtl). B, C, prepectoral spine from Sucuriju Creek outcrop, Pitinga Member of the Trombetas Formation, State of Pará, Brazil (specimen no. Cenpes 003-V). Scale: 10 mm.

On the other surface of the core sample (text-fig. 2C), the skeletal elements are much smaller or broken into small pieces. This may be due to the fact that the mode of deposition of these remains has varied during the formation of the bone-bed. This surface shows a large number of isolated scales and small dermal plates. Strangely enough, most scales are exposed in basal view, and show the classic gibbose base of acanthodian scales. Only one scale displays a well-preserved crown (h in text-fig. 2D), ornamented with a median boat-shaped ridge and lateral stepped zones.

Finally, a small dermal bone (g) with a vermiculate ornamentation may be either a plate of the sclerotic ring or a dermal bone of the cheek.

The isolated spine from the Sucuriju Creek (text-fig. 3B, C) is a large, flat prepectoral spine, ornamented with broad, somewhat sinuous noded ridges. The proximal half of these ridges bears a double row of nodes.

COMPARISON AND DISCUSSION

The presence of broad-based fin spines, prepectoral spines, and large intermediate ventral spines indicates a climatiid acanthodian. The ornamentation of spines (particularly that of the pectoral fin spine) and scales is very like *Ptomacanthus* Miles (Miles 1973, fig. 1A, pl. 4, 19) from the Lower Devonian (Gedinnian) of Europe. In contrast, the tooth whorl is not of climatiid type, but resembles that of the ischnacanthid *Gomphonchus* Gross (Gross 1967). The only differences concern the very large size, much shorter lateral denticles, and sinuous ridges on the main teeth in the Brazilian form.

Finally, the prepectoral spine of the Sucuriju Creek is of climatiid type, and matches the ones found in the borehole core, yet its double rows of tubercles on each ridge represent quite an unusual type of ornamentation.

Although climatiid and ischnacanthid acanthodians are known as early as the Late Silurian, this assemblage of large forms is rather suggestive of an Early Devonian acanthodian fauna. If the climatiid remains are to be referred to *Ptomacanthus*, a Gedinnian (Lochkovian) age would be preferable for this part of the Trombetas Formation.

It is noteworthy that these Brazilian acanthodian spines are strikingly similar to those recorded from a bone-bed in the Catavi Formation at Seripona, Bolivia (Goujet *et al.* 1984; Janvier and Suarez-Riglos 1986; Gagnier *et al.*, 1988). The Catavi Formation is regarded as Late Silurian in age, and the bone-bed at Seripona was originally referred to the Přidolian on the basis of lithostratigraphical correlations with *Clarkeia antisiensis*-bearing localities. However, its acanthodian and thelodont assemblage is rather suggestive of the Early Devonian (possibly Siegenian or even Emsian; Turner, *in* Gagnier *et al.*, 1988). This discrepancy in the dating of the Seripona bone-bed is hard to resolve, although one should note that thelodont scales have proved to be quite reliable stratigraphical fossils. Those from Seripona are inferred to represent a large species of *Turinia*, comparable to Early and Middle Devonian forms from Australia and Antarctica (Turner *in* Gagnier *et al.*, 1988). No thelodont scales of this genus have been recorded from the Silurian, yet thelodont scales are abundant as early as the Early Silurian.

STRATIGRAPHICAL COMMENTS

The discovery of these acanthodian remains may have a major bearing on the determination of the upper age limit of the Trombetas Formation. In fact, this has become a matter of concern in the last few years, since Quadros (1985A and B) assigned the upper section of that unit (the Pitinga and Manacapuru Members) from the Ludlovian/Gedinnian, upwards to the Siegenian, on the basis of acritarchs and chitinozoans; he revalidated the viewpoint of Ludwig (1964), who envisaged the possibility of a gradational contact between the Trombetas Formation and the overlying Devonian Maecuru Formation, based on sedimentological evidence. In contrast to Ludwig's view, an intervening unconformity (corresponding to the Wenlockian/Siegenian gap) has been conventionally recognized by most authors, according to whom the Trombetas Formation could be no younger than the Llandovery (Lange 1967, 1972; Daemon and Contreiras 1971; Caputo *et al.* 1972), or at most Wenlockian (Caputo 1984; Caputo and Lima 1984). Late Ordovician/Early Llandoverian (Medinian) age assignments for the Pitinga Member have long persisted in the literature, ever since the pioneer palaeontological and stratigraphical investigations of early workers (e.g. Derby 1878; Clarke 1899; Katzer 1903; Schuchert 1906; Maury 1929; Ruedemann 1929) had pointed out the occurrence of characteristic species in the local fauna, such as *Arthrophycus harlani* Conrad, *Climacograptus innotatus* Nicholson, and *Orthis callactis* Dalmann. However, further research has provided new evidence that is consistent with Quadros' interpretation. *Climacograptus*, for instance, is known to have survived into the Lower Devonian of Europe (see Jaeger 1979, for original reference). Current palynological investigations by Dr Jane Gray (University of Oregon, USA) strongly suggest that the spore assemblages of the Pitinga Member are of post-Llandoverian age, and the alleged *O. callactis* of Clarke (1899) turned out after closer inspection to be a generically indeterminable dalmanellid (A. J. Boucot, pers. comm. 1984, 1985).

The acanthodians discussed herein are certainly no older than the Upper Silurian (see discussion above); they occur only in highly bioturbated siltstones and sandstones that are regarded as belonging to the uppermost Pitinga Member (the only member of the Trombetas Formation present in the Trombetas valley, according to recent geological interpretations). These bioturbated, sometimes massive beds differ markedly from the underlying shales and sandstones of the Pitinga Member, and have been previously mapped by Enge-Rio geologists as the lower part of the Devonian Maecuru Formation (Jatapu Member). However, more recent palynological determinations by L. P. Quadros of the fish-bearing sediments from the cascade of the Sucuriju Creek revealed acritarch assemblages that are typical of the Pitinga Member (L. P. Quadros, pers. comm. 1986). Thus, the Jatapu Member is considered to be absent in this region, the Maecuru Formation being represented here only by its upper division, the Lontra Member, of Emsian/Eifelian age.

Unfortunately, little is known of the vertical distribution of critical taxa through the Trombetas section. The following remarks are based on preliminary field observations made in 1986 by J.H.G.M.

Less than 75 m below the bone-bearing interval of well SM-504, at the Viramundo waterfall (text-fig. 1), the lowermost Trombetas beds, resting on the crystalline basement, are finely laminated siltstones and shales charged with climacograptid remains. A few metres higher, downstream of the Viramundo waterfall, fine-grained sandstones, locally displaying a hummocky cross stratification, contains the invertebrate fauna described by Clarke (1899), which includes brachiopods (*Anabaia*, *Heterorthella*, etc.), similar to those of the Upper Silurian of Argentina, Paraguay, and Bolivia. These fossils may be collected at the northern end of the Boto and Praia Lisa Islands, the southern portion of Madame Island, and adjacent outcrops on the right bank of the river. Still higher in the column (that is, further downstream), abundant trace fossils referable to *Arthrophycus harlani* Conrad crowd the bedding planes of sandstone slabs exposed in a bluff at Caramujo locality, on the left bank of the Trombetas River.

None of the fossils mentioned above has been observed in association with the fish remains in the bioturbated rocks of the upper Pitinga Member; rather, they seem to be stratigraphically confined to lower beds of distinct lithology. In the Sucuriju Creek, scarce, poorly preserved *Arthrophycus*-like traces are found in sandstones exposed a few hundred metres upstream of the cascade outcrop (i.e. stratigraphically a few metres above it), where acanthodian remains occur, but these traces may represent a form other than *A. harlani* (A. J. Boucot, pers. comm. 1986).

CONCLUSIONS

Acanthodian remains from the Pitinga Member of the Trombetas Formation of northern Brazil suggest an Early Devonian (possibly Gedinnian) age. An Ordovician or Early Silurian age can be definitely ruled out for this section, but a late Silurian age is still possible.

Acknowledgements. The authors are indebted to Dr A. J. Boucot (Oregon State University, Corvallis, USA), Dr J. Gray (University of Oregon, Eugene, USA), and Dr L. P. Quadros (Petrobrás Research Center—Cenpes, Rio de Janeiro, Brazil) for having provided pertinent informations quoted in the text, and to Petrobrás—Petroleo Brasileiro S.A. for permission to publish this paper. English was corrected by Dr M. Pickford (Paris).

REFERENCES

CAPUTO, M. V. 1984. Stratigraphy, tectonics, palaeoclimatology and palaeogeography of northern basins of Brazil, 583 pp. Ph.D. thesis (unpublished), University of California, Santa Barbara, California.

—— and LIMA, E. C. 1984. Estratigrafia, idade e correlação do grupo Serra Grande. *An. 33e Congr. brasil. Geol.* **2,** 740–753.

—— RODRIGUES, R. and VASCONCELOS, D. N. N. 1972. Nomenclatura estratigráfica da bacia do Amazonas; histórico e atvalização. *An. 26e Congr. Brasil. Geol.* **3,** 35–46. Sociedade Brasileira de Geologia, Belém.

CLARKE, J. M. 1899. A fauna siluriana superior do rio Trombetas. *Arch. Mus. nacn.* **10,** 1–48.

COPPER, P. 1977. Paleolatitudes in the Devonian of Brazil and the Frasnian Famennian mass extinction. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* **21,** 165–207.

DAEMON, R. F. and CONTREIRAS, C. J. A. 1971. Zoneamento palinológico da bacia do Amazonas. *An. 25e Congr. brasil. Geol.* **3,** 79–88.

DERBY, O. A. 1878. Contribuções para a geologia da região do Baixo Amazonas. *Arch. Mus. nacn.* **3,** 77–104.

GAGNIER, P. Y., TURNER, S., FRIMAN, L., SUAREZ-RIGLOS, M. and JANVIER, P. 1988. The Lower Devonian vertebrate and mollusc fauna of Seripona, Chuquisaca, Bolivia. *N. Jb. geol. paläont. Abh.* **176,** 269–297.

GOUJET, D., JANVIER, P. and SUAREZ-RIGLOS, M. 1984. Devonian vertebrates of South America. *Nature, Lond.* **312,** 311.

GROSS, W. 1967. Uber das Gebiss der Acanthodier und Placodermen. *Jl Linn. Soc.* (*Zool.*), **47,** 121–130

GUIMARAES, D. 1964. *Geologia do Brasil*, 264pp. Minist. Minas e Energia, Rio de Janeiro.

JAEGER, H. 1979. Devonian graptolithina. *Spec. Pap. Palaeont.* **23,** 335–339.

JANVIER, P. and MELO, J. H. G. 1987. Late Devonian actinopterygian scales from the Upper Amazon Basin, north-western Brazil. *An. Acad. brasil. Ciênc.* **59,** 3.

—— and SUAREZ-RIGLOS, M. 1986. The Silurian and Devonian vertebrates of Bolivia. *Bull. Inst. Fr. Etud. and.* **15,** 73–114.

KATZER, F. 1897*a*. Das Amazonas-Devon und seine Beziehungen zu den anderen Devongebieten der Erde. *Sitzungsber. Kgl. böhm. Gesellsch. Wiss., Math.-naturwiss. Kl.* **46,** 1–50.

—— 1897*b*. A fauna devonica do rio Maecurú a as suas relações com a fauna de outros terrenos devonicos do globo. *Bol. Mus. Para. Hist. nat. ethnogr.* **2,** 204–246.

—— 1903. *Grundzüge der Geologie des unteren Amazonas-gebietes (des Staates Para in Brasiliens)*, 298 pp. Max Weg, Leipzig.

KEGEL, W. 1953. Contribução para o estudo do Devoniano da bacia do Parnaíba. *Bol. Div. Geol. Mineral.* **141,** 1–48.

—— 1957. Das Parnaiba-Becken. *Geol. Rundsch.* **45,** 522–540.

LANGE, F. W. 1967. Subdivisão biocstratigráfica e revisão da coluna siluro-devoniana de bacia do Baixo Amazonas. In *Atas Simp. sobre a Biota Amazonica*, **1,** 215–326, annex 1–4. Conselho Nacional de Pesquisas, Belém.

—— 1972. Silurian of Brazil. *Spec. pap. geol. Soc. Am.* **133,** 33–39.

LEONARDI, G. 1982. Descoberta da pegada de um anfíbio devoniano no Parana. *Ciênc. Terra*, **5,** 36–37.

—— 1983. *Notopus petri* nov. gen., nov. sp.: une empreinte d'amphibien du Dévonien du Parana (Brésil). *Géobios*, **16,** 233–239.

LUDWIG, G. 1964. Nova divisão estratigráfica e correlação faciológica por meio de pequenas estruturas internas dos sedimentos silurianos e devonianos da bacia do Medio Amazona s, 72 pp. *Petrobrás-Cenap (ciênc.-Téc.-Petrol., Seç. expl. Petrol., 1)*, Rio de Janeiro.

MAURY, C. J. 1929. Uma zona de graptolitos do Llandovery Inferior no rio Trombetas, Estado do Pará, *Brasil. Monogr. Serv. geol. mineral.* **7,** 1–53.

MENDES, J. C. 1971. *Geologia do Brasil*, 344 pp. Instituto Nacional do Livro, Rio de Janeiro.

MILES, R. S. 1973. Articulated acanthodian fishes from the Old Red Sandstone of England, with a review of the structure and evolution of the acanthodian shoulder-girdle. *Bull. Br. Mus. nat. Hist. (Geol.)*, **24,** 113–213.

QUADROS, L. P. 1985*a*. Distribução bioestratigráfica dos Chitinozoa e Acritarchae na bacia do Amazonas, 179 pp. Ph.D. thesis (unpublished), Universidade Federal do Rio de Janeiro, Rio de Janeiro.

—— 1985*b*. Natureza do contato entre as formações Trombetas e Maecurú (bacia do Amazonas). *In* CAMPOS, D. A., FERREIRA, C. S., BRITO, I. M. and VIANA, C. F. (eds.). *Coletânea de trabalhos paleontologicos*; trabalhos apresentados no VIII Congresso Brasileiro de Paleontologia, 1983, 435–441. DNPM-MME (Sér. geol., 27, Seç. paleont. estratigr., 2), Brasilia.

RUEDEMANN, R. 1929. Descripção dos graptolitos do rio Trombetas. *Monogr. Serv. geol. mineral.* **7,** 20–24.

SANTOS, R. S. 1961. Peixes fósseis do Devoniano Inferior de Picos, Estado do Piaui. *An. Acad. brasil. Ciênc.* **33,** 32.

SCHUCHERT, C. 1906. Geology of the Lower Amazon region. *J. Geol.* **14,** 722–746.

PHILIPPE JANVIER
U.A. 12 du C.N.R.S.
Institut de Paléontologie
8, rue Buffon
75005 Paris
France

JOSE HENRIQUE G. MELO
Petrobras/Cenpes/Divex/Scbipe
Cidade Universitaria, Qd. 7
Ilha do Fundao
21910 Rio de Janeiro
Brazil

Typescript received 25 May 1987
Revised typescript received 9 July 1987